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RESEMBLANCES AND CONTRASTS BETWEEN ZOOLOGIC AND PALÆONTOLOGIC RESEARCH IN MAMMALOGY. DESIRABILITY OF UNIFORM STANDARDS AND SYSTEMS IN CLASSIFICATION, IN DESCRIPTION, IN MEASURE- MENT, IN REASONING¹

BY HENRY FAIRFIELD OSBORN

In submitting this paper the author presented a model of the skull of *Eotitanops gregoryi*, the diminutive Eocene ancestor of all the titanotheres; a fossil skull of *Palaeosyops major*, an extremely short-headed titanothere; a fossil skull of *Dolichorhinus hyognathus*, an extremely long-headed titanothere; also, for comparison, recent skulls of a broad-headed bulldog and of a long-headed greyhound. He further submitted recent papers by several leading mammalogists, namely, Messrs. Allen,² Merriam,³ Osgood,⁴ and his own memoirs on the "Systematic Revision of the Equidæ"⁵ and the "Craniometry of the Equidæ,"⁶ as examples of resemblances and contrasts in palæontologic and zoologic methods.

¹ Paper presented by the author, under this title, at the meeting of the Society, May 3, 1920, in the American Museum of Natural History.

² Allen, J. A. Ontogenetic and Other Variations in Muskoxen, with a Systematic Review of the Muskox Group, Recent and Extinct. Mem. Amer. Mus. Nat. Hist., N. S. vol. I, part IV, March, 1913.

³ Merriam, C. Hart. Review of the Grizzly and Big Brown Bears of North America. North American Fauna, no. 41, February 9, 1918.

⁴ Osgood, Wilfred H. Revision of the Mice of the American Genus *Peromyscus*. North American Fauna, no. 28, April 17, 1909.

⁵ Osborn, H. F. Equidæ of the Oligocene, Miocene, and Pliocene of North America, Iconographic Type Revision. Mem. Amer. Mus. Nat. Hist., N. S. vol. II, part 1, May, 1918.

⁶ Osborn, H. F. Craniometry of the Equidæ. Mem. Amer. Mus. Nat. Hist., N. S. vol. I, part 3, June, 1912.

Mammalogy began as the science of mammalian life, of the structure of mammals as well as of their habits, of their classification based on existing life, of the changes shown in geographic distribution (Buffon). The founders of this science, Linnaeus and Buffon, naturally paid greater attention to external characters, to obvious osteological and dental characters, than to some of the internal characters. Buffon was impressed with the geographic variation of mammals. The older classification up to the time of Owen was based partly upon habits of feeding (e.g., Insectivora, Carnivora), and partly on external characters (e.g., Pachydermata). With Cuvier,⁷ deBlainville,⁸ and Owen⁹ began the more intensive study of the osteology and odontography of the mammals, together with the foundations of mammalian palaeontology as developed in the master hands of Cuvier and of Owen. Flower paid closer attention to the osteology of the mammals and did little to develop the odontography.

In the time of Darwin the subject divided into (a) the zoology and (b) the palaeontology of the mammals. This division has gradually led to different principles and methods of research based on the different nature of the materials, such as the absence of all soft parts, and the fragmentary nature of the hard parts in fossil mammals. An intensified and philosophic study of the hard parts became essential to progress.

The more recent tendency among palaeontologists is to bring these two branches together again (Lydekker, Scott, Wortman, Osborn, Matthew, Gregory, Gidley, Miller, and others). The first in this country to study the zoology of mammals on Darwinian principles, i.e., geographic and ontogenetic variation in color and form, was Allen (1876).¹⁰ The older school of vertebrate palaeontologists of this country, Leidy, Cope, and Marsh, worked almost exclusively on the osteology of the extinct mammals, but in his later years Cope developed the odontography by founding the tritubercular theory. He also

⁷ Cuvier, Georges L. C. F. D. *Recherches sur les Ossemens Fossiles de Quadrupèdes.* Tomes I-IV, 1812.

⁸ deBlainville, H. M. Ducrotay. *Ostéographie des Mammifères.* 1839-1864.

⁹ Owen, Richard. *Description of Teeth and Portions of Jaws of Two Extinct Quadrupeds (*Hyopotamus vectianus* and *H. bovinus*) . . . with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes.* *Quarterly Journal of Geol. Soc. of London*, vol. IV, 1848, pp. 103-141, pls. VII, VIII.

¹⁰ Allen, J. A. *The American Bison, Living and Extinct.* Mem. Mus. Com. Zool., Harv. Univ., vol. IV, no. 10, 1876.

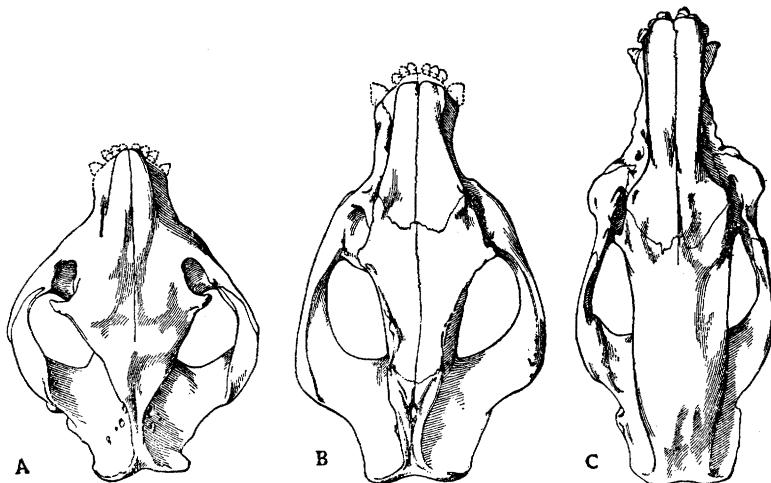


FIG. 1. SKULL PROPORTIONS AMONG TITANOTHERES

A, Brachycephaly, short-headed, *Paleosyops major*. B, Mesaticephaly, medium-headed, *Manteoceras manteoceras*. C, Dolichocephaly, long-headed, *Dolichorhinus hyognathus*.

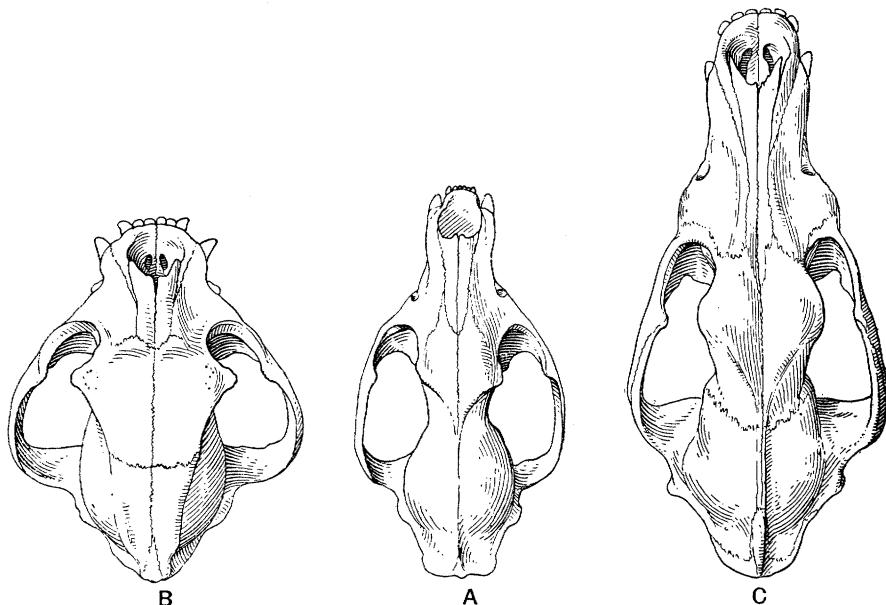


FIG. 2. SKULL PROPORTIONS AMONG CANIDÆ

A, Primitive, subdolichocephalic (*Daphænus hartshornianus*). B, Brachycephalic (bulldog). C, Dolichocephalic (Russian wolf-hound).

developed the mechanical interpretation of the bones and of the teeth in relation to function but without close regard to musculature. Marsh and Cope began to observe the phylogeny of the mammals. Marsh came near the truth in the phylogeny of the horse. Independently in Europe Gaudry¹¹ made great contributions to the phylogeny of the mammals. Kowalevsky (1872)¹² was the first to study the details of tooth and foot structure in relation to the Darwinian principles of adaptation, survival, and extinction.

Of the leading mammalogists of this country Allen followed his earlier observations on the pelage and other external characters by the intensive study of the variations of the skeleton, of the skull, and of the dentition in several groups of mammals, especially the bison and the muskoxen. In the former he took account of extinct forms. The present honored president of this Society, Merriam, has led the way in studying the skull intensively with its modifications in *relation to the function and distribution of the muscles*, in the rodents especially.

Many of the colleagues and junior workers of these two leaders have won distinguished success in the study of the geographic variations of the skull and skeleton, especially Miller, Osgood, Grinnell, and Hollister. One of the most marked evidences of the appreciation of this school of American research is the invitation to Miller by the Trustees of the British Museum to write the "Mammals of Western Europe,"¹³ a work now recognized in Europe as a classic.

The younger school of mammalian palaeontologists in this country, mostly of the school of Osborn and Scott, have made a distinct advance upon the work of Leidy, Cope, Marsh, Gaudry, and Kowalevsky in the following five directions:

I. Intensive study of the teeth, leading to the use of a new odontography of the Mammalia, based primarily on the tritubercular theory of Cope. This odontography in the hands of Osborn, Scott, Matthew, Gregory, and other colleagues has become the standard odontography of the Mammalia. It was founded upon the original studies of Osborn suggested by the original tritubercular theory of Cope; the homologies have been modified by studies of Gidley and Gregory; the terminology stands.

¹¹ Gaudry, Albert. *Les Enchainements du Monde Animal dans les Temps Géologiques Fossiles Primaires* (1883) and *Secondaires* (1890).

¹² Kowalevsky, W. *Sur L'Anchitherium Aurelianense Cuv. et sur L'Histoire Paléontologique des Chevaux. Mem. L'Académie Impériale des Sciences de St. Petérsbourg, VII^e Serie, tome XX, no. 5 et dernier.*

¹³ Miller, Gerrit S. *Mammals of Western Europe*, 1912. *Brit. Mus. Nat. Hist.*

II. Intensive study of the evolution of the living and fossil ungulate skull and skeleton and of the teeth by the means of indices (measurements of a single bone or tooth) and of ratios (comparative measurements of two bones or of teeth and bones). This has been especially the work of Osborn and of Gregory on the titanotheres and of Osborn on the horses. In the limbs, Cope (1889)¹⁴ adumbrated this idea. In 1900 Osborn¹⁵ worked out the angulation, which was developed by Gaudry (1906).¹⁶ R. C. Osburn (1906),¹⁷ a student of Osborn, applied the idea in aquatic adaptation. Matthew (1909)¹⁸ took up the limb-ratios of Carnivora in relation to weight and speed.

III. Phylogenetic intergradations of skeletal and tooth form as observed in the finely intergrading ascending and descending geologic stages of evolution. This has been the work of Osborn, Scott, Matthew, Granger, and Gidley in this country, and of Depéret in France.

IV. Application of the principles of mechanics to the muscles and evolution of the proportions of the limbs. This has been chiefly the work of Osborn and of Gregory. Gregory, especially, has developed the mathematical aspect of this subject and the means of restoring the musculature of extinct mammals.¹⁹

This method has been partly anticipated by the physical anthropologists, also by the leading students of animal motion. This extended investigation by Osborn and Gregory in perissodactyls, compared with amblypods and proboscideans, opens up principles which apply equally to all quadrupeds and bipeds, reptilian, avian, mammalian.

V. Substitution of a vertical phylogenetic or phyletic classification for the horizontal geographic classification of Linnæus, Flower, and Cope. Osborn, especially, has worked out this system of classification

¹⁴ Cope, E. D. The Mechanical Causes of the Development of the Hard Parts of the Mammalia. *Journ. of Morphology*, vol. III, pp. 137-290, 1889.

¹⁵ Osborn, H. F. The Angulation of the Limbs of Proboscidea, Dinocerata, and Other Quadrupeds, in Adaptation to Weight. *Amer. Nat.*, vol. XXXIV, pp. 89-94, 1900.

¹⁶ Gaudry, Albert. Fossiles de Patagonie. Les Attitudes de quelques Animaux. *Ann. de Paleontologie*, tome I, pp. 1-42, 1906.

¹⁷ Osburn, R. C. Adaptive Modifications of the Limb Skeleton in Aquatic Reptiles and Mammals. *Ann. N. Y. Acad. Sci.*, vol. XVI, no. 9, part III, pp. 447-482, March 1, 1906.

¹⁸ Matthew, W. D. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, vol. IX, part VI, 1909.

¹⁹ Gregory, W. K. Notes on the Principles of Quadrupedal Locomotion and of the Mechanism of the Limbs in Hoofed Animals. *Ann. N. Y. Acad. Sci.*, vol. XXII, pp. 267-294, 1912.

in the rhinoceroses and horses, as well as in other perissodactyl families and in the proboscideans. This mode of classification has been more or less widely accepted. The most debatable point is the adoption of the special family term ending in *-inae* for the phylum. For example, the family of rhinoceroses is divided by Osborn into six phyla,²⁰ each of which is assigned a subfamily name. Similarly Osborn divides the Proboscidea into six phyla,²¹ each of which takes a subfamily name. Some of these subfamilies or phyla are shown to be extremely ancient, to go back millions of years, e.g., the long-jawed phyla of the Proboscidea, which goes back to the Lower Oligocene.

In the case of the titanotheres, extending over more than a third of the Tertiary period, the family is subdivided into twelve subfamilies or phyla, which are separated by *distinct evolutionary tendencies* leading to different extremes of structure.

In mammalian palaeontology Merriam, Lull, Loomis, and Stock have been advancing both the phyletic and zoogeographic methods of research.

In the meantime equally intensive observations have been made by Osgood, Grinnell, Nelson, G. M. Allen, Bailey, Howell, and other mammalogists on two very important principles of mammalogy, namely:

1. Intensive study of the relation of geographic distribution and vertical range on proportional characters of the skull and skeleton, and on the color characters of the pelage.
2. The linking up of distinct geographic forms through geographic connecting intergrades. The special paper to which I allude is the paper by Osgood on *Peromyscus*.

The latest phase of zoologic mammalogy in this country is seen in the work of Sumner²² in attempting to analyze the variations of *Peromyscus* from the standpoint of the mutation theory of DeVries, of

²⁰ Osborn, H. F. Phylogeny of the Rhinoceroses of Europe. *Rhinoceros Contributions* no. 5. Bull. Amer. Mus. Nat. Hist., vol. XIII, art XIX, pp. 229-267, Dec. 11, 1900.

²¹ Osborn, H. F. A Long-Jawed Mastodon Skeleton from South Dakota and Phylogeny of the Proboscidea. Bull. Geol. Soc. Amer., vol. 29, no. 1, pp. 133-137, Mar., 1918.

²² Sumner, F. B.

The Rôle of Isolation in the Formation of a Narrowly Localized Race of Deer-Mice. Amer. Nat., Vol. LI, pp. 173-185, March, 1917.

Genetic Studies of Several Geographic Races of California Deer-Mice. Amer. Nat., Vol. XLIX, pp. 688-701, Nov., 1915.

Continuous and Discontinuous Variations and Their Inheritance in Peromyscus. Amer. Nat., Vol. L, pp. 1-16, Jan., 1919.

Mendelism, and of modern genetics, as well as from the older standpoint of geographic and climatic variation.

One of the newer aspects of field and museum work is the careful notation and emphasis on habit, habitat, and environmental relations, as developed in the Congo collections of the American Museum of Natural History and the publications thereon by Lang and Chapin.

SUMMARY

In the above very imperfect review, which does not pretend to mention all the notable workers nor all the various fields of work, it is seen that there has been a gradual and entirely natural *divergence* between *zoologic* and *palaeozoologic* workers in mammalogy. It is obviously desirable to bring these workers together and to select the most consistent and philosophic methods from each. Such a union is now in progress in the joint researches of Gidley (a palaeontologist) and Miller (a zoologist) on the phylogeny, evolution, and classification of the Rodentia.

All these observers and natural philosophers are treating exactly the same animal—the mammal—from different points of view. Yet in reading some of their writings and comparing them with my own, I am reminded of the old East Indian fable of the blind men and the elephant. Each of the blind men formed an entirely different opinion of the character of the elephant from the particular part of the animal's anatomy on which his hand rested, namely, trunk, tusk, the limb, the chest, etc.

My desire in the present communication is to point out that these different modes and methods of research which have sprung up independently among zoologists and palaeontologists should be harmonized. It is important that zoologists and palaeontologists should read each other's papers, speak the same language, and use the same terminology. It is important that they should use similar methods of measurement, similar indices and ratios, similar terms in the nomenclature of the teeth and of the skeleton. I am confident that such harmonic methods will be developed, especially among the younger members of this Society, such as Anthony and Camp, who have been trained both in the school of zoology and of palaeontology.

myseus. Amer. Nat., Vol. LII, pp. 177–208; 290–301; 439–454, April–Sept., 1918.

Autonomy of the Tail in Rodents. Biological Bulletin, Vol. XXXIV, pp. 1–6, Jan., 1918.

Several Color "Mutations" in Mice of the Genus *Peromyscus*. Genetics, vol. 2, pp. 291–300, May, 1917.

PRINCIPLES AND NOMENCLATURE OF PROPORTION CHARACTERS

I have recently pointed out that in mammals the larger percentage of the characters employed in specific and subspecific description are *proportion characters* and *color intensity characters*. The remaining smaller percentage are *new characters* or *presence and absence characters* (see Miller's "Mammals of Western Europe").

As a beginning, we mammalogists might adopt one system of observation and description in the matter of the proportions of the skeleton and of the skull and unify the different modes of description which prevail at present as, for example, in Miller's "Mammals of Western Europe," in Merriam's recent studies of the bears of North America,²³ in researches on limbs and skulls of ungulates of Osborn, and in the craniology introduced by Osborn of the horse and of the titanotheres.

In respect to limb proportion also, recent discoveries by Osborn and Gregory among the ungulates show that the very precise proportions expressed by indices and ratios enable us to divide the ungulates into ambulatory, submediportal, mediportal, and graviportal types, and into cursorial and subcursorial types. These are convergent or homoplastic types quite irrespective of ancestry. For example, a horse and an antelope, capable of carrying the same body weight at the same speed, exhibit exactly similar indices and ratios in their limbs. These similar proportions are adaptations to speed and weight which evolve quite irrespective of family lines.

SIX DIVERSE CAUSES OF VARIATION

Another principle of skeletal proportion also requires reconsideration from the standpoint of the newer biological studies enumerated by Osborn in his recent work, "The Origin and Evolution of Life," in which the close relation of the proportions of various parts of the body to the internal secretions of the endocrine glands is demonstrated. The principal endocrine glands are the interstitial (sex), the thyroid, the thymus, the pituitary, the suprarenal, the pineal; all are now known to influence growth and development. For example, the proportion of the pelvis in the horse has a direct relation to the secretion of the interstitial tissues of the sex glands; a stallion pelvis has different proportions from that of a gelding, as well as from that of a mare.

²³ Merriam, C. H. Review of the Grizzly and Big Brown Bears of North America. North American Fauna, no. 41. 1918.

Consequently, differences which have been classed and lumped together in long tables of measurement hitherto as *variations of proportion* may be now analyzed as partly due to one or more of a great number of different causes, namely:

- (1) Proportions due to differences of habit and modes of locomotion.
- (2) Proportions due to differences of nutrition, kinds and habits of feeding.
- (3) Proportions due to normal differences of sex, male and female.
- (4) Proportions due to internal or endocrine secretions, e.g., of the male and female sex glands.
- (5) Proportions due to adaptive changes during age and growth correlated with precocity or helplessness in the young, and juvenile, mature, and senescent development of the sex glands.
- (6) Proportions due to the withdrawal of the internal secretions after the natural close of the activity of the sex glands.
- (7) Proportions due to compensatory growth.

First: it is obvious that older systems of measurements, which lumped all measurements together as "variations," irrespective of cause, lacked such analysis of the *causes of proportion*. Second: it is clear that many of the differences that have been treated as hereditary variations—as material for natural selection—are not variations at all in the true sense of the term, but are really adaptations to seven or more different sets of causes which vary with conditions of life. Third: we have reason to suspect that the mean fluctuating variations of size and proportion may be mere individual and ontogenetic phenomena, noninheritable, and consequently without bearing on racial evolution.

Compensatory changes of proportion are often profoundly important. For example, it has been shown that a dog with the fore limb experimentally removed tends to develop *saltatorial proportions* in the hind limbs, by way of compensation for the loss of the fore limb, that is, to imitate the springing type of limb, e.g., the hare. It follows that ontogenetic changes in hind limb proportion may be brought about through defects in fore limb proportion.

I have reached the opinion that if we could eliminate these seven or more causes of modification and variation, and measure a very large number of similar bones (the pelvis, for example) of animals of (1) the same habits, (2) the same food, (3) the same sex, (4) the same intensity of endocrine secretion, (5) the same age, (6) the same sexual stage, (7) of exactly the same strain or race, there would be a *standard length and breadth*. I believe that nature tends to *standardize every bone in all pure breeds and to eliminate variations in proportions*. Otherwise

we should not observe such uniform powers of rapid locomotion in wild herds of mammals and wild flocks of birds. Consequently a large part of the elaborate *tables of variation* signify little except that there is an *incessant change of proportion in every bone of the body from birth to death*, some of which is adaptive, some accidental or fortuitous, some really hereditary and significant. Nor is there any single part of the skeleton which can be taken as a norm or base by which other parts can be measured. This is not inconsistent with the fact that skeletal *indices* and *ratios* based on animals of the same sex and same age may constitute excellent subspecific and specific characters, and may also be much more reliable in definition than the present descriptive terms "longer," "shorter," "broader," "deeper," etc. As good a definition of a race, of a subspecies, or of a species, as any other, would be a number of its indices and ratios taken from different parts of the skeleton. It appears that direct measurements are profoundly altered by gigantism and dwarfing, but indices and ratios remain the same. Again Allen (1887) has led the way by applying the method of ratios in his discussion of the skeletal characters of *Monachus* in comparison with three other phocids. In his paper on *M. tropicalis*²⁴ he presented comparative ratios for the skull (pp. 11, 12, with table), skeleton and limb segments (pp. 12-17) with important and suggestive results.

CONCLUSION

In this paper I have pointed out only a few of the many resemblances and contrasts between zoologic and palaeontologic research in mammalogy. The palaeontologist who does not study living mammals is out of date; the modern palaeontologist is constantly studying living mammals to supplement his limited material in tooth and bone and to check his constructive imagination as regards habits and habitat. The zoologist who does not study fossil mammals fails to perceive some of the most fundamental processes of mammalian evolution. For by a strange paradox, which I have pointed out many times, every character in a living mammal appears to be static or in a state of rest,²⁵

²⁴ Allen, J. A. The West Indian Seal (*Monachus tropicalis* Gray). Bull. Amer. Mus. Nat. Hist., vol. II, pp. 1-34, April, 1887.

²⁵ "Within historical times we have absolutely no evidence of serious evolutionary change. A system that would have sufficed for three thousand years in the past will probably do for an equal time in the future. By the time evolutionary change introduces serious disturbance in the present scheme of things it is probable that our whole classification system will have been scrapped for something better or else altered beyond recognition."—P. A. Taverner: The Test of the Subspecies. Jour. Mamm., vol. I, no. 3, p. 125, May, 1920.

while every character observed in a phylum of extinct mammals is found to be kinetic or in a state of motion.

Palæontology reveals many other paradoxes, unsuspected by zoology. For example, unprotected animals which may be breeding very rapidly and varying widely, like the mice, may be evolving very slowly, while highly protected mammals which are breeding slowly, like the elephants, may be evolving very rapidly. In these and many other animals, as recently pointed out by Conklin, there is an inverse ratio between the law of selection (survival and elimination) and the rate of adaptive evolution. This shows that in Nature evolution is not hastened by rapid breeding and selection, but that rapid evolution may be due to other causes.

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A NOTE ON THE HABITS OF THE TIMBER WOLF

BY CHARLES EUGENE JOHNSON

Opportunities for close-up view of the wild timber wolf in action are, I believe, sufficiently rare to justify submitting the following notes.

The summer of 1912 was spent in making some studies and collections of mammals in northern Lake County, Minnesota, in a portion of the Superior National Forest. The evening of September 1, my companion, Harold N. Hanson, and I, traveling by canoe, returned to one of our main camps after a four days' absence in a more remote locality. As we pulled up at our landing place, which was at the upper end of a rapids and about half a mile from our camp, we observed numerous wolf tracks in the mud along the river bank; these had not been there when we left camp a few days before. But it was now after sundown and too late for further investigation.

The next day a strong northwest wind was blowing and at 3:30 in the afternoon, taking a couple of large traps and my rifle, I set out to discover if possible the meaning of the many wolf tracks. Upon approaching the landing place I moved very cautiously, more as a matter of habit than with any expectation of seeing anything unusual. Just before emerging into the open space by the landing I caught the sound of gentle splashing in the water and, peering through a little opening in the bushes, I saw a timber wolf in the river, stationary, but rising and falling as if "treading water" and taking savage bites at a large body